

# Development of Spatial Coarse-to-Fine Processing in a Model with Cortical Feedback

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## Abstract

Coarse-to-fine processing, in which the general features of a stimulus are processed before more detailed structure, is a fundamental mode of information transmission in many neural sensory systems, including the visual pathway. Originally thought to be a cortical process, spatial coarse-to-fine processing has recently been documented in both the retina and the lateral geniculate nucleus (LGN). Here, we have considered the developmental aspect of dynamic spatial frequency tuning in the LGN. We use data from LGN neurons from three age groups: adult cats and kittens at 4 and 8 weeks post-natal to construct a firing-rate based thalamocortical model. Our model includes both feedforward and feedback components of the circuit. We consider how developmental changes in spatiotemporal structure affect feedforward thalamic contribution to cortical SF tuning, as well as the efficacy of cortical feedback in facilitating this dynamic. Our results indicate that kittens early in the developmental process are more strongly affected by corticothalamic feedback than adults. This implies that these recurrent connections may be an important mechanism in facilitating the development of spatial coarse-to-fine processing. We propose an experimentally testable hypothesis for the function of the extensive feedback in the corticothalamic circuit, and provide an ideal framework within which to further explore this process through more computationally intensive simulations.

## Introduction

The mode of information processing in neural sensory systems has been the subject of many experimental and computational studies. The sequential analysis of information, where coarse features are processed before fine details, has been described in several sensory systems, including the auditory (Narayan et al., 2005) and somatosensory (Sripati et al., 2006) pathways. In the visual system, the existence of coarse-to-fine processing is intuitive—when looking quickly at a scene, we process the general features before focusing on individual objects. Indeed, this dynamic has been documented for several tuning parameters in vision, including orientation selectivity (Ringach et al., 1997; Shapley et al., 2003; but see also Gillespie et al., 2001; Müller et al., 2001; Mazer et al., 2002), spatial frequency selectivity (Bredfeldt and Ringach, 2002; Mazer et al., 2002; Frazor et al., 2004; Nishimoto et al., 2005) and binocular disparity tuning (Ringach, 2003; Menz and Freeman, 2003). In particular, spatial frequency (SF) tuning provides insight into visual perception, especially within

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the framework of the coarse-to-fine system. Low spatial frequencies convey global information about an image (such as general orientation or proportion), whereas finer detail (such as edges) is provided by higher spatial frequency information (Bar, 2004).

Though initially thought to be primarily a cortical function, spatial coarse-to-fine processing has been observed in the retina and lateral geniculate nucleus (LGN) in mature animals (Enroth-Cugell et al., 1983; Allen and Freeman, 2006). However, the developmental aspect of coarse-to-fine processing has yet to be studied. The SF tuning dynamics in the thalamus have been shown to largely be a consequence of the center-surround organization in LGN spatiotemporal receptive fields (Allen and Freeman, 2006), the structure of which evolves significantly during maturation.

In adults, the cortical dynamic can be largely attributed to feedforward contribution from the LGN (Allen and Freeman, 2006). In our study, we consider how the developmental changes in the structure of LGN receptive fields (RFs) affect this contribution. In addition, as there exists a massive number of feedback projections to the thalamus from the visual cortex, we also examine the effect of corticothalamic feedback on dynamic SF tuning.

Though the significant amount of cortical feedback is a striking feature of the visual pathway, a definitive role for these connections has not been agreed upon. Experimental studies investigating the effect of cortical feedback require isolation of specific inputs in a complex circuit, and despite several such studies (Cudeiro and Sillito, 1996; Sillito and Jones, 2002; De Labra et al., 2007; Andolina et al., 2012), the function of these connections remains elusive. In our study, we consider the contribution from both feedforward and feedback components in the thalamocortical loop to help elucidate the function of the recurrent corticothalamic connections.

In our study, we consider how the spatial coarse-to-fine process in the central visual pathway differs in various stages of development. We present a simple model to examine the development of dynamic SF tuning in the thalamocortical circuit. Using results from electrophysiological experiments in cats (Cai et al., 1997), we map the RFs of “average” LGN cells from three age groups: mature cats, and kittens at 8 and 4 weeks postnatal. We then use these RFs to construct a feedforward-feedback thalamocortical model to determine how changes in the structure of the spatiotemporal RFs of LGN cells affect the cortical coarse-to-fine dynamic during the maturation process. Because our model includes both feedforward and feedback features, we also evaluate how the role of recurrent cortical input in facilitating this dynamic varies throughout the developmental process. Our results suggest a function for the significant amount of recurrent connections to the thalamus from the visual cortex.

## Model

To investigate the contribution of the LGN to the cortical coarse-to-fine dynamic during development, we construct a phenomenological thalamocortical model with feedforward and feedback connections. We analyze how developmental changes in the LGN spatiotemporal receptive field (RF) affect the cortical coarse-to-fine process by comparing results from simulations using characteristic RF structure from mature cats and 4- and 8-week postnatal kittens (Cai et al., 1997). Although previous studies have suggested that cortical SF tuning in mature animals is largely accounted for by purely feedforward contributions (Allen and Freeman, 2006), this process has never been examined thoroughly during development. Furthermore, a large number of recurrent corticothalamic connections have been

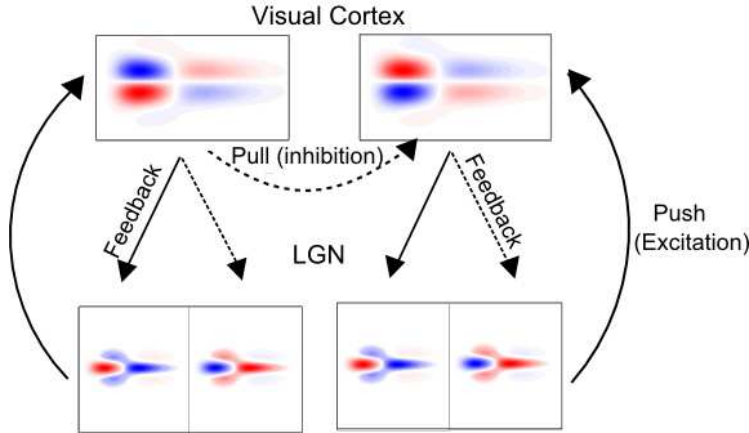


Figure 1: Schematic of our feedforward-feedback model. Solid and dashed lines indicate excitatory and inhibitory connections, respectively. Thalamic cells (bottom) connected to a cortical cell (top) have overlapping receptive fields (RFs); the offset between LGN RFs has been exaggerated for clarity in this figure. In all spatiotemporal contour maps presented, red and blue contours enclose bright and dark excitatory regions, respectively.

shown to exist, but there are few answers as to what purpose they serve (Alitto and Usrey, 2003; Briggs and Usrey, 2008).

We use a firing-rate based model which does not consider structural and biophysical mechanisms that would likely be implemented in a cell based model. However, comparison of a similar conceptual model to more realistic simulations using integrate-and-fire neurons (Troyer et al., 1998) showed that while the addition of these mechanisms may affect exact numerical calculations, they do not alter not the qualitative results. We have omitted these mechanisms to reduce the number of free parameters and make the results easier to interpret.

We consider responses only from non-direction-selective layer IV simple cells which receive input from LGN cells with central RFs and biphasic temporal structure. We do not differentiate between LGN X and Y cells in our model as they have been shown to exhibit similar linear RF organization (Cai et al., 1997). In our simulations, excitatory feedforward input to the cortex is provided by 40 spatially-offset LGN cells, and inhibition is given by 40 LGN cells with identical position and opposite phase through a cortical interneuron. Cortical cells, in return, provide feedback (either excitatory or inhibitory dependent on a tuning parameter) to the thalamus. We consider responses from a cortical simple cell after twenty simulated runs through a corticothalamic feedback loop. A schematic of the model can be found in Figure 1.

The spatiotemporal receptive field (RF) relates a neural response  $r(t)$  to a stimulus  $S(x, t)$ . Assuming the neural system is time-invariant, a linear estimate of the response is given by (Heeger, 1991):

$$\hat{r}(t) = \iint \text{RF}(x, t') S(x, t - t') dx dt'. \quad (1)$$

The spatiotemporal receptive field corresponds to the responses of a cell to test spots which

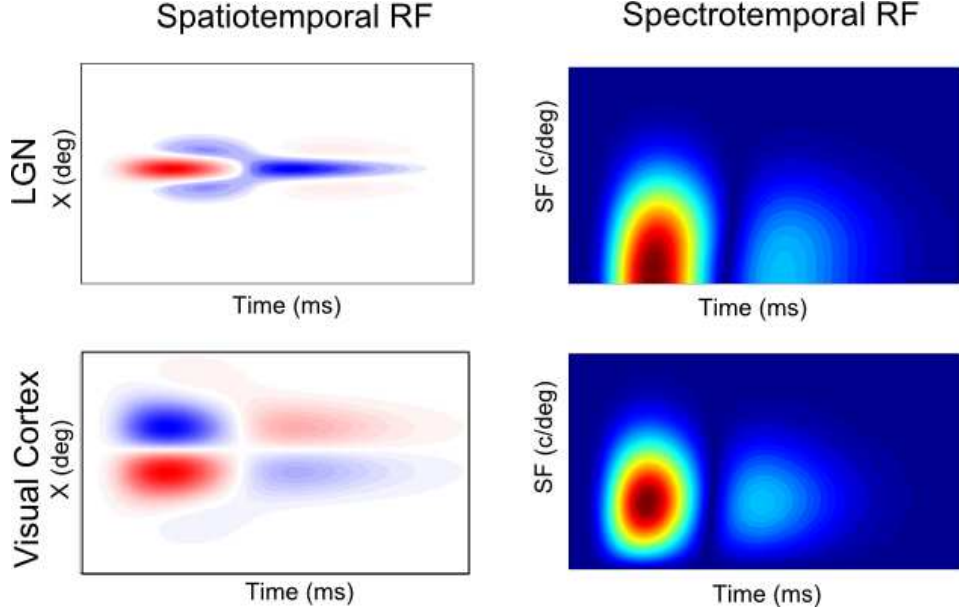


Figure 2: Representative spatiotemporal (left) and Fourier-transformed spectrotemporal (right) receptive fields from LGN (top) and visual cortex (bottom). Rightward tilted contours in the spectrotemporal RF indicate the presence of coarse-to-fine processing.

are both very small in space and very brief in time. We use a Fourier transform to reformulate the spatiotemporal RF function in the spatial frequency (SF) domain. Spectrotemporal receptive fields predicted using Fourier analysis have reproduced the SF tuning dynamics of directly measured RFs in previous studies (Allen and Freeman, 2006). The Fourier-transformed spectrotemporal receptive field can then be interpreted as the response of a cell to sinusoidal gratings of frequency  $f$  and phase  $\phi$ . Examples of simulated spatiotemporal and spectrotemporal receptive fields from LGN and visual cortex are shown in Figure 2.

We choose spatiotemporal receptive field functions and their parameters based on average fits to results from previous studies. The RFs of cortical simple cells in V1 are traditionally mapped as Gabor functions (DeAngelis et al., 1993). A two-dimensional Gabor function is a Gaussian kernel modulated by a sinusoid. For simplicity, we model simple cell RFs to have two explicit subregions, separated by  $1^\circ$ , in accordance with data from previous studies (Allen and Freeman, 2006). Flanking subregions due to the surround response in the LGN are also often present (see Figure 2).

LGN cells have a center-surround antagonistic structure (Cai et al., 1997). A popular choice for modeling thalamic relay cells is to consider the receptive field to be spatiotemporally separable, and to model the spatial part using a difference of Gaussians (DOG) model. In our construction, when there is no cortical feedback, LGN RFs consist of two components corresponding to the center and surround responses. The peripheral area (“surround”) responds oppositely to light than the central region. We consider two types of LGN cells: ON- and OFF-center cells. ON-center cells are stimulated when light is shined on the center, and inhibited when light is shined on the surround. OFF-center cells display the opposite

pattern.

We model LGN spatiotemporal RFs based on characterizations from Cai et al. (1997). LGN RFs are described by the expression:  $\text{RF}(x, t) = F_c(x)G_c(t) - F_s(x)G_s(t)$ , where  $F(x)$  and  $G(t)$  are spatial and temporal profiles respectively, and subscripts  $c$  and  $s$  correspond to center and surround responses. Note that the complete spatiotemporal RF will be space-time separable if there is no delay between center and surround ( $\tau_d = 0$ ) and inseparable if there is a nonzero delay ( $\tau_d > 0$ ). Temporal filters for the center and surround are given as difference of gamma functions:

$$G_c(t) = K_1 \frac{c_1(t-t_1)^{n_1} e^{-c_1(t-t_1)}}{n_1^{n_1} e^{-n_1}} - K_2 \frac{c_2(t-t_2)^{n_2} e^{-c_2(t-t_2)}}{n_2^{n_2} e^{-n_2}}, \quad (2)$$

and  $G_s(t) = G_c(t - \tau_d)$ .

Parameters for spatial and temporal profiles were largely chosen based on model fits in Cai et al. (1997). Temporal profiles were shown to vary significantly throughout the maturation process—in particular, the center-surround delay  $\tau_d$  progressively decreases during development.

We describe spatial profiles using an extended difference of Gaussian (eDOG) model, which reduces to the familiar (DOG) model when there is no cortical feedback. The eDOG model is derived from a mechanistic model for an impulse-response function for the thalamic relay cell (Einevoll and Plesser, 2011). From this function, the spatial receptive field for an LGN cell is described as

$$F_{c,s}(x) = \frac{1}{(2\pi)^2} \int e^{ikx} \frac{A_c e^{k^2 \sigma_c^2/4} - A_s e^{-k^2 \sigma_s^2/4}}{1 - C e^{-k^2 a^2/4}} dk. \quad (3)$$

Here,  $A_c$  and  $A_s$  are the amplitudes of center and surround responses,  $2\sigma_c$  and  $2\sigma_s$  are the sizes of these responses, and  $k$  is the wavenumber corresponding to the spatial frequency  $f$  by  $k = 2\pi f$ . The feedback parameters  $C$  and  $a$  determine the strength and spatial spread of the feedback, respectively.

The RF center and surround size do not vary significantly with age, but the ratio of their amplitudes  $A_s/A_c$  increases significantly throughout development (Cai et al., 1997). We vary  $C$  within the range  $C \in (-1, 1)$  and fix  $a = 0.075$ . Our range for  $C$  was chosen so as to lie within the constraints of our approximation (described below). The value for spatial spread  $a$  was chosen to qualitatively support results involving corticothalamic feedback—namely, that it serves to strengthen the antagonistic surround response (Alitto and Usrey, 2003; Briggs and Usrey, 2008; Andolina et al., 2012) but does not have large effect on the size of the surround response (Andolina et al., 2012).

We use circularly symmetric Gaussians to model the cortical feedback because for low cortical feedback strength, the equation can be approximated as a sum of DOGs. This form allows it to be more readily interpretable in this familiar context. In our simulations, we use an approximation of the model as follows (see Einevoll and Plesser (2011) for a detailed derivation). Using a series expansion,  $1/(1-y) = \sum_{m=0}^{\infty} y^m$ , with  $y = C e^{k^2 a^2/4}$  and replacing the denominator term of the above integral expression, we arrive at our equation of LGN spatial profiles:

$$F_{c,s}(x) = \sum_{m=0}^{\infty} C^m \left( A_c \frac{e^{-x^2/(\sigma_c^2 + ma^2)}}{\pi(\sigma_c^2 + ma^2)} - A_s \frac{e^{-x^2/(\sigma_s^2 + ma^2)}}{\pi(\sigma_s^2 + ma^2)} \right). \quad (4)$$

This equation is an infinite sum of DOGs, and the first term of this sum ( $m = 0$ ) is very similar to the traditional feedforward model. The following terms correspond to “corrections” of this direct term due to  $m$  rounds of the corticothalamic loop. In our simulations, we truncate this sum at the twentieth-order term, since higher terms are essentially equal to 0 for all values of  $|C|$  we consider. This series uniformly converges for  $|C| < 1$ ; see e.g., Einevoll and Plesser (2011).

The properties of the LGN cell population are also determined from previous experimental results. Because cells with larger RFs have been shown to exhibit shorter latencies, we shift the temporal profile along the time axis by adjusting parameters  $t_1$  and  $t_2$ , by a function of the size of the RF (Weng et al., 2005):

$$\text{shift} = \text{STC} \left( \pi \frac{d_c^2}{2} - \pi \frac{d_m^2}{2} \right), \quad (5)$$

where  $d_c$  is the center diameter of the thalamic cell, and  $d_m$  is the median center diameter from the distribution ( $1.15^\circ$ ) (Allen and Freeman, 2006). We multiply these values by a space-time constant ( $\text{STC} = -3.5$ ) to obtain a population of LGN cells with latencies similar to experimental values reported by Alonso et al. (2001).

The position of each cell is drawn from a normal distribution with mean equal to the center of the cortical subregion and standard deviation  $0.15^\circ$  (Alonso et al., 2001). LGN RF center sizes are drawn from a normal distribution centered at a value equal to the width of the subregions, because it has been shown that the size of RF centers of LGN cells are typically equal to or slightly greater than the width of the cortical subregion they project to (Alonso et al., 2001). From this, we calculate the size of the RF surround as  $\sigma_s = 1.5 \times \sigma_c + 0.4$  (Cai et al., 1997). More details on these calculations can be found in the literature (Allen and Freeman, 2006).

Each cortical subregion receives input from 20 ON- and OFF-center LGN neurons (i.e., a cortical cell receives input from 40 LGN cells, which is within the rough range for the number of geniculate cells converging onto a cortical simple cell given by Alonso et al. (2001)). We calculate input to a model cortical cell as the sum of rectified impulse-response functions from each LGN cell to static sinusoidal gratings at SFs between 0.001 to 1.5 cycles/degree and four different phases. In addition to input from the thalamus, the excitatory cortical cell receives weighted input from the inhibitory cortical cell. We treat processing of LGN input by the inhibitory cell as linear for simplicity. The total input to the excitatory cell is then:

$$I(f, \phi, t) = \text{LGN}_e(f, \phi, t) - W \times \text{LGN}_i(f, \phi, t - \tau), \quad (6)$$

where  $\text{LGN}(f, \phi, t)$  are the firing rates of the thalamic neurons,  $W$  is the inhibition weight, and  $\tau$  is a delay to account for the transmission of the impulse. We calculate the output of the excitatory cell as the input integrated with a time constant of 10 ms and rectified. To calculate tuning parameters, we consider an analysis window beginning and ending when the SF variance rises and falls to 20% of the maximum value (Allen and Freeman, 2006). We calculate SF shifts as an average value from 100 trials for each parameter set.

## Results

While the coarse-to-fine dynamic was originally thought to be a primarily cortical process, recent studies have shown its existence in the early visual pathway. Allen and Freeman (2006) provided evidence that feedforward contribution from the thalamus accounts largely

for cortical dynamic SF tuning observed in mature animals (Bredfeldt and Ringach, 2002; Frazor et al., 2004; Mazer et al., 2002). However, the developmental aspect of this process has not yet been studied. In the following, we consider how changes in the structure of LGN spatiotemporal RFs during maturation affect dynamic SF tuning, as well as how the contribution of corticothalamic feedback to the coarse-to-fine dynamic evolves throughout development.

Structural properties of the spatiotemporal RF of thalamic relay cells have been indicated as a significant contributor to the cortical coarse-to-fine process. In particular, both experimental and modeling studies have implicated the antagonistic relationship between center and surround responses in LGN cells (Enroth-Cugell et al., 1983; Allen and Freeman, 2006). In their developmental study, Cai et al. (1997) characterized changes in LGN RF organization by analyzing spatiotemporal receptive fields from thalamic cells of adult cats and 4- and 8-week postnatal kittens. In our study, we consider two of the structural aspects of the center-surround relationship which were shown to significantly change during development: the length of center-surround delay and the relative surround strength.

The results of Allen and Freeman (2006) suggested that the length of delay between center and surround has an effect on SF shift. Another parameter that we believe may be influential to this dynamic is the ratio of the strengths of the center and surround responses. In addition, cortical feedback to the LGN has been suggested to strengthen the antagonism of the surround response. We analyze how the coarse-to-fine process changes as LGN spatial and temporal profiles evolve, as well as how cortical feedback affects dynamic SF tuning at each developmental stage.

From our simulations, we calculate tuning shifts from estimates of peak SF, using an analysis window beginning and ending when the SF variance rises and falls to 20% of the maximum value. A cell’s optimal SF ( $SF_{\text{peak}}$ ) at time  $t$  is the SF at the peak of the tuning curve. SF shift is then defined as the log ratio of final and initial values of  $SF_{\text{peak}}$ :

$$\Delta SF = \log_2 \frac{SF_{\text{peak}}(t_{\text{final}})}{SF_{\text{peak}}(t_{\text{init}})}. \quad (7)$$

We choose spatiotemporal RF parameters based on model fits in Cai et al. (1997). Values for the delay between center and surround responses in all simulations are based on averages for each age group,  $\tau_d = 16\text{ms}$  for 4-week old kittens,  $12\text{ms}$  for 8-week old kittens, and  $8\text{ms}$  for adult cats. We change relative surround strength  $A_s/A_c$  among age groups by keeping the amplitude of the center response constant and varying the surround amplitude.

In Figure 3, we show results of our simulations. Figure 3A shows the effects of various surround-center ratios ( $A_s/A_c$ ) on coarse-to-fine processing. Simple cell spatiotemporal RFs (Figure 3A, middle panel) are modeled with two primary subregions, and flanking subregions tend to develop due to the surround response. Representative cortical simple cell RFs are shown in the middle panel for both very low (left) and very high (right) center-surround ratios. For low values of  $A_s/A_c$ , there are no flanking regions observed in the cortical RFs. As  $A_s/A_c$  increases, a strong surround is clearly seen in the LGN RFs (Figure 3A, top panel), as well as in the cortical RFs. At very high ratios, primary subregions no longer dominate the flanking subregions in the cortex.

The effect of the  $A_s/A_c$  ratio on cortical SF shift for each age group is shown in the bottom panel of Figure 3A. All three age groups exhibit a monotone increase in SF shift at low values of  $A_s/A_c$ . At the average values of  $A_s/A_c$  reported by Cai et al. (1997) ( $A_s/A_c = 0.3, 0.2, 0.1$  for adults, 8-, and 4-week old kittens, respectively), the mean peak shift was 0.52 octaves for adults, 0.42 octaves for 8-week old kittens, and 0.31 octaves for

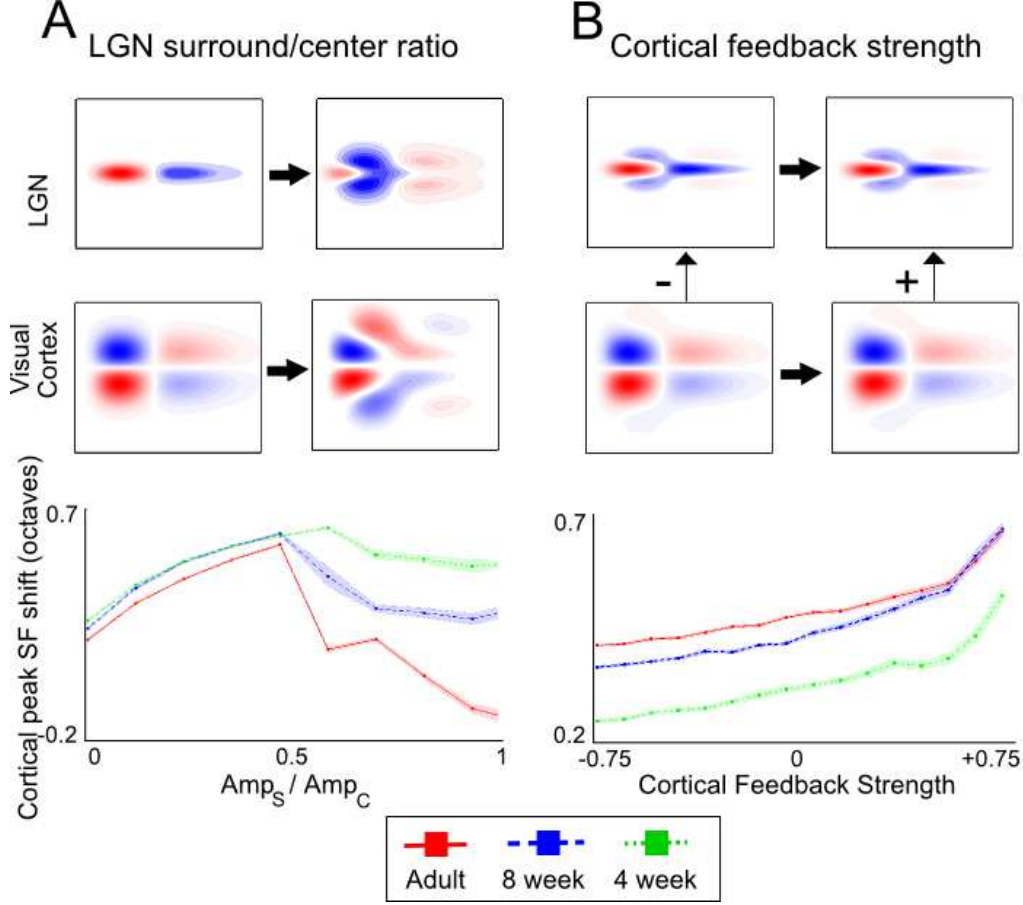


Figure 3: Effects of selected model parameters on SF tuning in the visual cortex. Top panels show representative LGN and cortical spatiotemporal RFs at the low and high end of the intervals considered for each parameter. Plots (bottom) display cortical peak SF shift for various values of the parameter for each age group. Each point corresponds to the mean taken from 100 simulations of our thalamocortical model, and shaded regions enclose  $\pm 1$  SEM away from the mean. Results for adults are shown in red, for 8-week old kittens in blue, and for 4-week old kittens in green. Center-surround delays for each age group are taken from estimates in Cai et al. (1997) in all simulations ( $\tau_d = 8, 12, 16$  for adults, 8-week and 4-week old kittens, respectively). **A**, Cortical peak SF shift as a function of surround-center ratio. Cortical feedback parameters are set to zero in this set of simulations. **B**, Cortical peak SF shift as a function of cortical feedback strength  $C$  (in arbitrary units). The spatial spread of the cortical feedback  $a$  was fixed at 0.075 (in arbitrary units). Surround-center ratios were as reported in Cai et al. (1997) for each age group ( $A_s/A_c = 0.3, 0.2, 0.1$  for adults, 8- and 4-week old kittens, respectively.)



4-week old kittens. All values were significantly different from each other ( $p < 0.001$  between 4-week old kittens and older age groups,  $p < 0.05$  between 8-week old kittens and adults).

As the ratio  $A_s/A_c$  increases, the peak SF shift for each age group reaches a maximum and begins to decline. Mature cats display a lower maximum SF shift (0.57 octaves) than both 8-week (0.60 octaves) and 4-week old kittens (0.62 octaves). These values were all significantly different from each other ( $p < 0.001$  for all comparisons). In addition, this maximum is reached at a lower ratio ( $A_s/A_c = 0.50$ ) than in kittens at 4 weeks ( $A_s/A_c = 0.60$ ).

We also consider how cortical feedback affects spatial frequency tuning in these two groups. A large number of recurrent corticothalamic connections have been shown to exist, but there are few answers as to what purpose they serve (Alitto and Usrey, 2003; Briggs and Usrey, 2008). Though only excitatory corticothalamic connections exist, inhibitory feedback via thalamic interneurons has been observed (Alitto and Usrey, 2003). For this reason, we consider a variety of feedback strengths ranging from strongly negative ( $C = -0.75$ ) to strongly positive ( $C = +0.75$ ).

In Figure 3B, we consider the effect of corticothalamic feedback on SF tuning shift. When  $C < 0$ , all aspects of the RF are tightly modulated, but the relative surround strength is effectively increased because the center response is suppressed more strongly. As  $|C|$  decreases and  $C$  approaches 0, the modulation is lowered, as is the strengthening of the surround. When  $C$  crosses 0 to represent dominant excitation, both features seen in dominantly inhibitory feedback are present: overall modulation and selective enhancement of the surround. However, the overall suppression is less strong when  $C > 0$  than for inhibitory strengths for equivalent values of  $|C|$ .

For dominantly inhibitory feedback, high  $|C|$  (strong feedback) results in lower shifts, with a monotonically increasing trend in SF shift as feedback strength approaches 0. This is because even though the relative surround strength effectively is raised when  $C < 0$ , the overall suppression is too strong for this enhancement to have an effect. All three age groups are affected relatively equally. At  $C = 0$ , there is effectively no feedback.

However, for dominantly excitatory feedback strengths, even though there is still an overall modulation, it is low enough such that the enhancement of the surround may have a positive effect on spatial dynamics. Therefore when  $C > 0$ , all three age groups show a rise in tuning peak shift as  $|C|$  increases.

Furthermore, we find that feedback is not equally effective in facilitating dynamic SF tuning in all age groups. Dominantly excitatory cortical feedback appears to have a heightened effect on the coarse-to-fine process during development when compared to its effect in mature cats. When cortical feedback is mainly inhibitory ( $C < 0$ ) or weakly excitatory ( $C > 0$ ,  $|C|$  small), there is a distinct difference in peak SF shift between age groups. However as feedback becomes more strongly excitatory, this disparity is reduced. When  $|C|$  is sufficiently high, no significant difference is seen between peak SF shifts in 8-week old kittens (blue line) and mature cats (red cats). Changes in SF shift with respect to  $C$  between age groups were found to be significantly different through a repeated-measures ANOVA at  $\alpha = 0.05$ .

## Discussion

Though coarse-to-fine processing has been implicated as a fundamental coding strategy in the visual pathway, the development of this process has not yet received much consideration.

In mature animals, dynamic spatial frequency tuning has been shown to be intimately linked with the center-surround organization in the receptive fields of LGN cells. We have studied how documented changes in the structure of the spatiotemporal RFs of LGN cells impact the cortical coarse-to-fine dynamic throughout the developmental process. Our thalamocortical model considers how differences in center-surround organization in kittens affects the feedforward contribution of thalamic cells observed in adults (Allen and Freeman, 2006). In addition, by considering both feedforward and feedback features, we also analyze how the efficacy of cortical feedback in facilitating this dynamic varies during development. Our results point to a possible functionality for the large number of recurrent corticothalamic connections in the development of dynamic spatial frequency tuning.

Our main result concerns the non-monotone relationship between relative surround strength and shift in tuning peak, suggesting the existence of an optimal center-surround balance which maximizes SF shift. Furthermore, this “optimal balance” occurs at different surround-center ratios throughout development. We found that kittens at 4-week postnatal favored the highest relative surround strengths and mature cats the lowest. Previous data have shown that on average, LGN cells from adult cats exhibit a higher surround-center ratio than those from kittens (Cai et al., 1997). Taken together with our results, this suggests that the surround-center ratios of mature animals are distributed close to or around their “optimum”, while the distribution for kittens is centered at a ratio significantly lower than their peak value. This implies that a corresponding increase in relative surround strength would have a proportionately larger effect on the peak tuning shift in kittens than in adults.

A mechanism which has been shown to heighten the antagonistic effect of the surround response is cortical feedback (Alitto and Usrey, 2003; Briggs and Usrey, 2008; Andolina et al., 2012). There is a very substantial amount of cortical thalamic connections that must be assumed to have clear functional implications. Feedforward connections from the thalamus to the visual cortex can account for coarse-to-fine dynamics in adults, but our results indicate that cortical feedback may participate in dynamic spatial processing during development. Cortical feedback to the LGN has been shown to have both excitatory and inhibitory effects, with little further knowledge as to the nature of this balance. For this reason, we have considered various feedback strengths, ranging from strongly inhibitory to strongly excitatory. When feedback is mainly inhibitory, all age groups show equivalent decreases in spatial frequency shift, which is presumably due to strong overall suppression of the RF. For dominant excitatory feedback, SF tuning shifts in kittens are preferentially increased so that they approach levels observed in mature animals.

Although experiments that clearly demonstrate how cortical feedback manifests in LGN cell responses require precise removal of corticothalamic connections and are therefore extremely complex, some studies have attempted to elucidate the effect of these connections. The extended difference-of-Gaussians (eDOG) model (Einevoll and Plesser, 2011) has qualitatively accounted for the results from several such experiments. However, as the direction of the excitatory-inhibitory balance of corticothalamic connections has not been fully characterized and is very unlikely to be static, we cannot conclude that a fixed set of parameters for this model will be universal. The inhibitory eDOG model has been shown to be in accordance with the experimental results of Cudeiro and Sillito (1996) and Sillito and Jones (2002). These experiments, however, primarily utilized circular patch-gratings of various sizes, whereas the receptive fields we have considered in this paper are derived from full-field moving bar stimuli. Additionally, other experiments involving inactivation of recurrent connections have found results in line with dominant excitation (De Labra et al., 2007). The parameters chosen for the excitatory eDOG model in this study qualitatively reproduce

structural properties observed in RFs with an intact feedback circuit, namely an increased center size and a higher surround-center ratio when compared to RFs of decorticate animals (Andolina et al., 2012). The kitten distributions observed in experiments by Cai et al. (1997) display larger centers than adults, which are consistent with higher levels of cortical feedback relative to adults. Kittens also display larger surround size, which was not implicated by Andolina et al. (2012) as an effect of feedback. However, surround size in kittens may appear larger due to the increased variation and noise observed in juvenile RFs (Cai et al., 1997).

In general, our model does not account for all of the complexities in the thalamocortical loop. Our use of a simple linear loop involving a single population of simple cells to describe corticothalamic feedback assumes direct input to all cortical populations from relay cells. Though it is true that the dominant input to the cortex from the LGN is in layer IV, there is also evidence of direct geniculate input to layer VI, where corticothalamic feedback is known to originate (Sherman and Guillery, 2001). Furthermore, experiments by Grieve and Sillito (1995) have shown that simple cells make up the majority of layer VI projections to the LGN. Additionally, our model is largely conceptual, and does not include several aspects which would be implemented in a computational model, such as intracortical connections between simple cells with similar RF structure, non-deterministic firing rates, or spike thresholds. However, comparison of a similar conceptual model to more realistic computational simulations Troyer et al. (1998) showed that the addition of these mechanisms may affect exact numerical results, but not the qualitative outcome.

Because of the clear importance of the recurrent connections to the thalamus from the cortex, there have been several studies, both experimental and computational, involving the analysis of corticothalamic loops. However, a conclusion about the functional role of the corticothalamic pathway has yet to be reached. Experimental studies must precisely and specifically inactivate or remove corticothalamic connections in order to be able to make definitive claims about the nature of cortical feedback. Techniques such as lesions or ablation (Murphy and Sillito, 1987), pharmacological blockage (Rivadulla et al., 2003), and transcranial magnetic stimulation (De Labra et al., 2007) have been used for this purpose. The results of these studies are neither in full agreement nor unequivocal in interpretation, possibly because these techniques tend to act on large areas of the cortex and cannot comment on more localized effects. Previous theoretical models have made use of the network structure of the corticothalamic circuit (Köhn and Wörgötter, 1996; Wörgötter et al., 1998; Hayot and Tranchina, 2001; Yousif and Denham, 2007), making their results difficult to interpret in a physiologically relevant way due to the sheer number of parameters.

The extended difference-of-Gaussians model, presented first by Einevoll and Plesser (2011), has a far more tractable structure, with only two biologically meaningful parameters:  $C$ , corresponding to the strength of the feedback, and  $a$ , corresponding to the spatial spread of the feedback. We have implemented this simplified representation of cortical feedback into a push-pull thalamocortical model in order to comprehensively analyze the development of the spatial coarse-to-fine process. All other parameters used in our model were taken directly from fits to experimental data (Cai et al., 1997).

Our observations of structural changes in the spatiotemporal RF of thalamic relay cells during development point out a particular susceptibility of kittens in the early stages of development to mechanisms which increase relative surround strength. Our results suggest that the LGN may use recurrent corticothalamic connections to “learn” the coarse-to-fine dynamic during development. In addition to vision, coarse-to-fine processing has been demonstrated in other sensory and motor systems (Narayan et al., 2005; Sripathi et al., 2006)

suggesting that it is a basic feature of neural circuitry. It is not far-fetched to postulate that the massive number of recurrent connections to the LGN function, at least in part, to facilitate the development of this process.

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